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A COMPARATIVE STUDY OF THORACIC AND CHELIPED MUSCLE ASYMMETRY IN MALE FIDDLER CRABS (GENUS: *UCA*)

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Abstract

Asymmetries in thoracic and leg muscles that move the single huge major cheliped of male fiddler crabs are compared to their contralateral homologues in nine species of *Uca*. In *Minuca* (*U. longisignalis, U. minax, U. pugnax,* and *U. rapax*) and *Boboruca* (*U. thayeri*) species, the major side body muscles are twice as large as the minor muscles, with more muscle fibers. Additionally, the individual sarcomeres are exceptionally long, reaching over 20 μm in length. In contrast, in species of the sub-genus *Celuca* (*U. crenulata, U. panacea, U. pugilator,* and *U. speciosa*), while these muscles may be up to six times larger than their contralateral homologues, with fibers nearly twice as long, the sarcomeres are not so hypertrophied.

Major muscles in the chela can be 20 times larger than their contralateral homologues. The largest chela muscles also show exceptionally large sarcomeres among *Minuca,* but not in *Celuca.*

It is shown that sarcomere lengths are inversely correlated with the speed and duration of the courtship wave behavior.

Introduction

Investigations of neuromuscular mechanisms associated with motor activities in animals have demonstrated the correlations between contractile fiber types, motor innervation, and their functional role in behavior. Crustaceans are especially favorable material for such studies due to the parsimony of their motor innervation (Atwood, 1972, 1973). Additionally, in some crustaceans the first pair of thoracic chelipeds, or claws, are bilaterally asymmetrical, consisting of a minor or relatively unspecialized chela and a major or more specialized contralateral chela. The neuromuscular basis of such asymmetry in the paired claws have been extensively studied in lobsters (review by Govind, 1984) and snapping shrimps (review by Mellon, 1981) and such studies provide fertile material for correlating neuromuscular specializations with behavior.

Perhaps the most flamboyant example of claw asymmetry is found in male fiddler crabs (Ocypodidae: genus *Uca*) in which the major claw is up to 20 times larger than the minor claw and may weigh almost as much as the rest of the animal. This major claw is used primarily for sexual and agonistic displays and interactions. Stereotypic waving (Crane, 1957, 1975; Salmon and Atsaides, 1968a, b), or sound production (Salmon, 1965, 1967; Salmon and Atsaides, 1969) by the major chela plays an important role in sexual behavior and in maintaining reproductive isolation (Salmon *et al.,* 1978), at least in some sub-genera of *Uca* (see Salmon, 1984). The major chela muscles, including those in the thorax, would be expected to show specialization as

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Non-standard abbreviations: CL: carapace length; L_P = posterior levator muscle; ML: manus length; R: range; SD: standard deviation.

compared to those of the minor chela of the male or to the symmetric small chelae of the female. Since these display waves and acoustic signals are species-specific, comparisons between species of *Uca* provide valuable material to determine whether such behavioral differences between closely related species can be correlated with differences in the morphological and physiological characteristics of the muscles responsible for the behavior.

In fiddler crabs, knowledge of the mechanisms underlying the ontogeny of chela asymmetry is still incomplete. In the first post-larval crab stages the chelae are small and symmetrical (Morgan, 1923). In many species handedness is determined by chance at an early post-larval stage (Morgan, 1924; Vernberg and Costlow, 1966, Feest, 1969; Yamaguchi, 1977), as in lobsters, while in others right handedness is specified (Yamaguchi, 1977; Barnwell, 1982). At the muscle fiber level, asymmetry occurs early in post-larval life in *U. pugnax,* coincident with the first sign of chela hypertrophy (Trinkaus-Randall and Govind, 1985). Asymmetry in *Uca* is irreversible once it is established.

This paper reports fiber characteristics of muscles of the chelae of seven species of North American fiddler crabs, representing three of the seven sub-genera of *Uca* established by Crane (1975). It is shown here that sarcomere lengths (as estimated by A-band measurements) of certain muscles that move the fiddler crab major chela are inversely correlated with the speed and duration of the courtship wave display. Furthermore, certain fiddler crab chela muscles, and especially those from members of the sub-genus *Minuca,* show exceptionally large sarcomeres (*e.g.,* over 20 μm in *U. minax*).

Materials and Methods

Animals

Species examined here and collection sites are as follows: *Uca (Minuca) minax,* Poquosin, Virginia and Fort McCalister State Park, Georgia; *U. (Minuca) pugnax,* Poquosin, Virginia; *U. (Minuca) rapax,* Sugarloaf Key, Florida; *U. (Minuca) longisignalis* (Salmon and Atsaides, 1968a) Panacea, Florida; *U. (Celuca) pugilator,* Panacea, Florida; *U. (Celuca) speciosa,* Big Torch Key, Florida; *U. (Boboruca) thayeri,* Fort Myers Beach, Florida. Several other species were examined less extensively: *U. (Celuca) panacea* (Novak and Salmon, 1974), Panacea, Florida, and *U. (Celuca) crenulenta,* Southern California. All of the crabs used were in intermolt (*circa* Drach stage C_4).

Experimental procedures

Animals were cold anesthetized (30 min on ice) and measurements of carapace length (CL), carapace width, and manus length (ML), from the heel of the propus to the tip of the pollex, were made with a vernier caliper (±0.1 mm). The side of the major claw, right or left, was also noted. The carapace was removed and the animal was immersed in seawater (25‰) chilled to 0°C, where removal of viscera and connective tissue was completed. The major and minor claws were secured in positions effecting unstressed extension of the muscles to be examined. For levators and remotors the claws were pinned forward and down, for promotors and depressors the claws were secured upward and back. For limb muscles the claw was secured either in the completely flexed position for stretcher and extensor muscles, or in the completely extended position for bender and flexor muscles. FAA fixative chilled to 0°C, a mixture of 30% ethanol, 7% formalin, and 3% acetic acid in water, was first injected with a hypodermic syringe into the region of the muscles, followed by immersion of the entire

preparation in fixative for 8–12 h. After transfer to 30% ethanol, muscles were removed to water. Whole muscle weights of thoroughly blotted muscles were made with a Cahn model RTL electrobalance. To obtain muscle "fibers," muscles were teased apart with sharpened watchmakers' forceps. In this study the term "fiber" refers to a relatively discrete bundle of fibrils; these may or may not have been muscle fibers derived from individual cells. Such fibers were mounted on glass microscope slides in a mounting medium (7 g gelatin and 50 ml glycerol in 50 ml water).

Light microscopy

Measurements were made of A-band lengths rather than of entire sarcomeres, as the former are less affected by moderate stretch or contraction (Franzini-Armstrong, 1970). These measurements were made for each fiber with an optical micrometer using phase contrast optics (25× ocular; 100× Zeiss Neofluor oil immersion objective). The slide was moved on the microscope stage until the fiber to be measured was centered in the illuminated beam from the condenser; the objective was then rotated into position and the first discrete A-band encountered was chosen for measurement. This measurement, close to the center of the fiber, was taken as the estimate for that fiber. For thoracic muscles such an estimate was made for every fiber, but for the larger extensor and stretcher limb muscles A-band measurements were taken for every fifth mounted fiber. To prevent inadvertent bias slides were labeled with numbers from a random number table and then mixed, before measurements were taken.

Variability in A-band length within muscle fibers (Franzini-Armstrong, 1970) was determined by measuring a series of A-bands in single fibers (see Results, *Variability of muscle fibers,* below). It was quantified by using the Coefficient of Variation (CV), the standard deviation (SD) divided by the mean ($\bar{X}$) times 100. The statistical significance of differences in means, for A-band lengths of muscles of the major side compared to their minor side homologues, was determined using the one-sided student's *t*-test. The Spearman Rank Correlation Coefficient (rs) was used to test correlations of wave duration and A-band lengths in different species (Siegel, 1956).

In those cases where sarcomere lengths were used, they were measured similarly with a Zeiss Neofluor 40× objective and 25× ocular. The length of a row of five consecutive sarcomeres was measured. The average length was taken as the estimate of sarcomere length for the fiber.

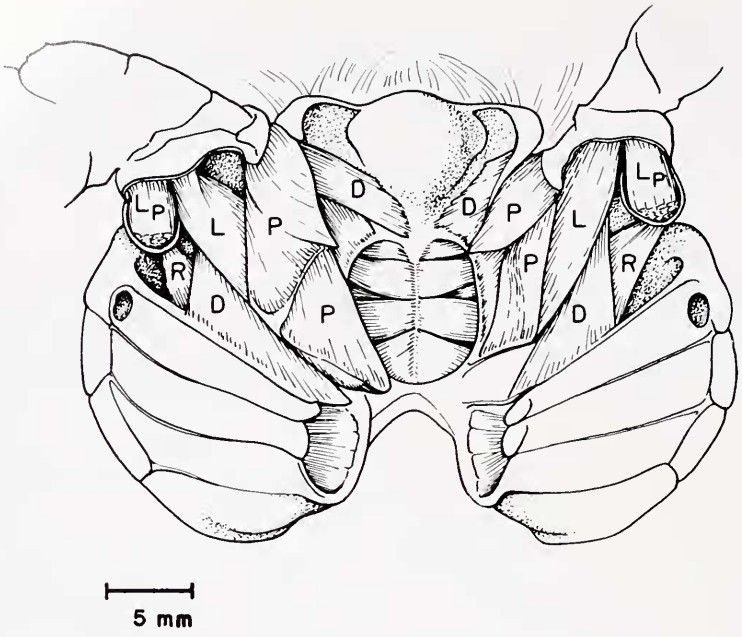
Results

Thoracic muscles of the cheliped segment

The thoracic musculature of two representative *Uca* species is shown from the dorsal side in Figure 1, with the major chelae on the left side in both cases. The four main thoracic cheliped muscles, the levator/depressor pair and the promotor/remotor pair, move the chelae up/down and forward/backward respectively. They are the primary thoracic muscles that move the major chela in the display wave. Arrangement of the muscles and skeletal elements are similar to those described for the portunid crab, *Callinectes sapidus* (Cochran, 1935).

The species of fiddler crabs examined could be divided into two groups according to the relative size and arrangement of the muscles of the major side. One group, species of the sub-genus *Celuca,* is exemplified by *U. pugilator.* The other group, represented by *U. minax,* includes all of the other sub-genera examined.

Table I shows the differences in weight between the major and minor side thoracic muscles of five individual crabs, and the weight ratios between the two sides. The



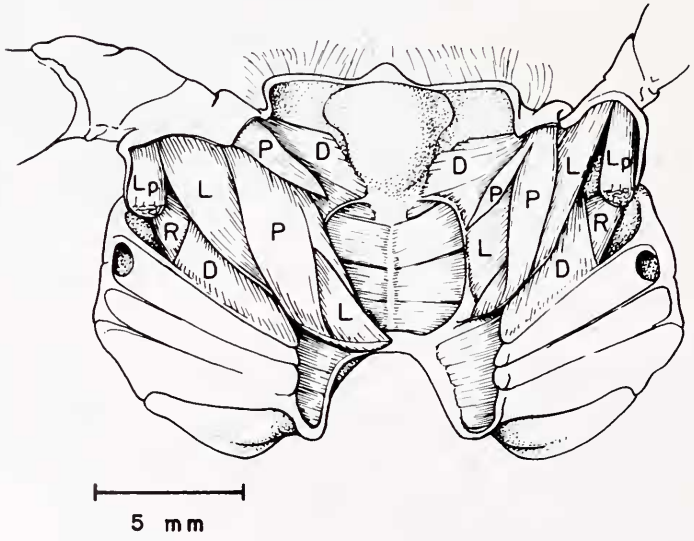


FIGURE 1. Muscles of the cheliped segment in adult male *Uca minax* (upper figure) and *U. pugilator* (lower figure), viewed from the dorsal side after removal of the dorsal carapace and viscera. The major chela is on the left in both drawings. Muscles: Promotor (P), Levator (L), Posterior Branch of Levator (Lp), Remotor (R) and Depressor (D).

mean of the major to minor side weight-ratios for the two *U. pugilator* levator muscles, 6.43, is significantly greater than the equivalent mean ratio for two *U. minax* and one *U. pugnax*, 2.78. But with the exception of this larger size, of variable extent for the different thoracic chela muscles, and consequently a more posterior extension of muscle attachments, the muscles of the major sides resemble those of the minor sides in all of the animals examined.

Measurements of A-band lengths taken from mounted thoracic chela muscle fibers also show differences between members of the subgenera *Celuca* and *Minuca* as well as differences between the major and minor sides. The data is most complete for fibers from the levator muscle. Figures 2 and 3 show data for males of seven species, as well as from a single female *U. minax*. With the exception of *U. pugilator* these typify the dramatic differences ($P < 0.005$) in fiber composition between the major and minor levator muscles seen for the 20 individual males where data were obtained from both sides, or between male major and female chelae from *U. minax*.

The representatives of the subgenera *Minuca* and *Boboruca* in Figure 2 possess fibers with exceptionally long A-bands. *U. minax*, in particular, has many fibers with A-bands in the range of 12–14 μm. These would correspond to resting sarcomere lengths of 20 μm or more (Fig. 4), among the longest sarcomeres recorded from striated skeletal muscle in any animal.

The relationships between major and minor levators of *U. pugilator* (sub-genus *Celuca*) are variable. A-band distributions for three representative males (Fig. 3) show means and distributions for the major levators that are very similar, but by comparison the means of the minor levators are inconsistent among individuals. In one individual *U. pugilator*, the lower figure, the minor levator muscle has a greater mean A-band length than that of the major levator. In only one of these three examples (the middle figure in Fig. 3, left) was the difference between mean A-band lengths of major and minor levators significant. Major and minor levator muscles from seven other male *U. pugilator* showed similar variable relationships between the muscles of the major and minor chelae. The other species of *Celuca*, *U. speciosa*, shown in Figure 3, right,

TABLE I

Weights (mg) of major side and minor side thoracic muscles which manipulate the chelae, from five individual Uca

Species	CL	Major/minor thorax muscle weights (major/minor ratio)			
		Levator	Depressor	Promotor	Remotor
U. minax	20.7	27.8/10.5 (2.7)	24.9/12.0 (2.1)	22.4/11.2 (2.0)	22.3/8.4 (2.7)
U. minax	19.9	26.2/8.5 (3.1)	15.4/10.4 (1.5)	14.6/6.6 (2.2)	14.4/7.5 (1.9)
U. pugnax	13.5	15.6/6.0 (2.6)	12.0/6.1 (2.0)	9.1/3.8 (2.4)	10.3/4.0 (2.6)
U. pugilator	13.8	18.9/2.6 (7.3)	13.9/3.8 (3.7)	3.8/1.7 (2.2)	6.6/3.0 (2.2)
U. pugilator	14.7	25.2/4.5 (5.6)	13.6/5.8 (2.3)	6.3/3.3 (1.9)	7.9/3.6 (2.2)

CL = carapace length (mm); the "ratio" values, weight of the muscle of the major side divided by weight of the homologous contralateral muscle, are shown in parentheses below each weight value.

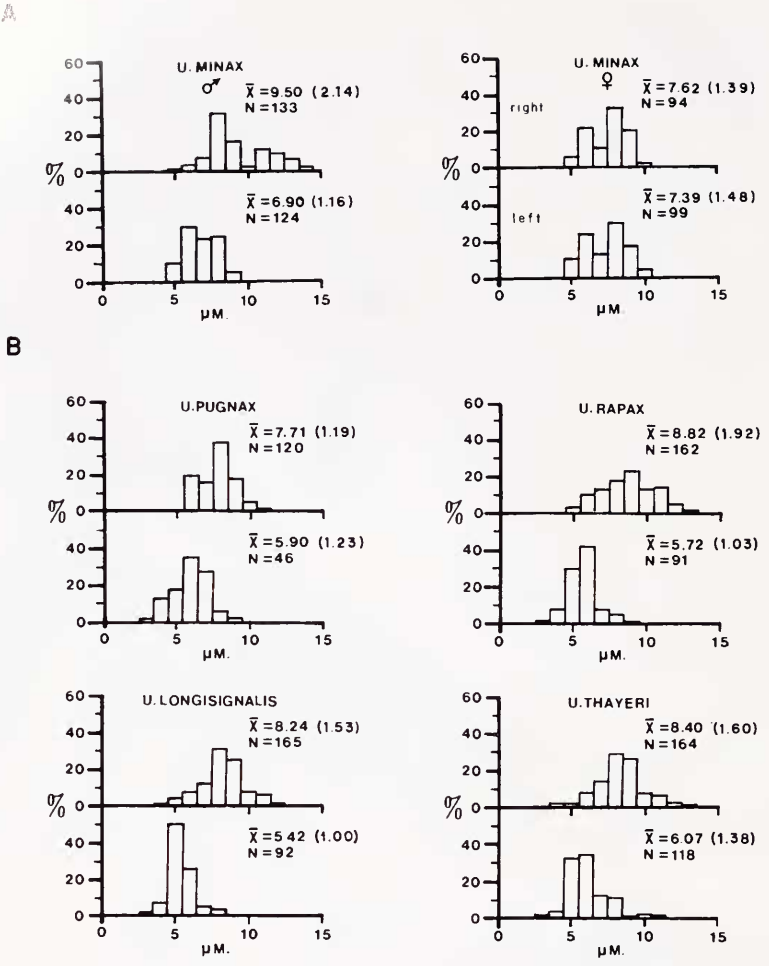


FIGURE 2. Comparisons of A-band lengths in major (upper figures) and minor (lower figures) levators of representative *Uca* of the subgenera *Minuca* and *Boboruca*. A: male *U. minax* (CL = 19.0 mm); female *U. minax* (CL = 20.2 mm). B: *U. pugnax* (CL = 12.0 mm), *U. longisignalis* (CL = 15.7 mm), *U. rapax* (CL = 13.5 mm) and *U. thayeri* (CL = 16.8 mm). $\bar{X}$ = mean A-band length (and SD) in μm from measurements of N fibers.

has a similar, less dramatic, asymmetry, with mean A-band lengths of 5.19 μm and 4.65 μm for the major and minor levator muscles (significant at 5% level).

Table II summarizes data from representative remotor muscles from seven species of *Uca*. Comparisons were made between homologous major and minor muscles of the same individual except in *U. pugilator* where it was necessary to compare muscles from two male crabs of similar size. These muscles of the major sides, including those of *U. pugilator*, had fiber populations with greater mean A-band lengths than those of the minor sides. All comparisons of means were highly significant ($P < 0.005$).

Data for both major and minor depressor and promotor muscles were taken for two species, *U. minax* and *U. pugilator*, and reflected similar asymmetry in fiber composition. For example, in a male *U. minax* (CL = 19.4 mm) means of A-band

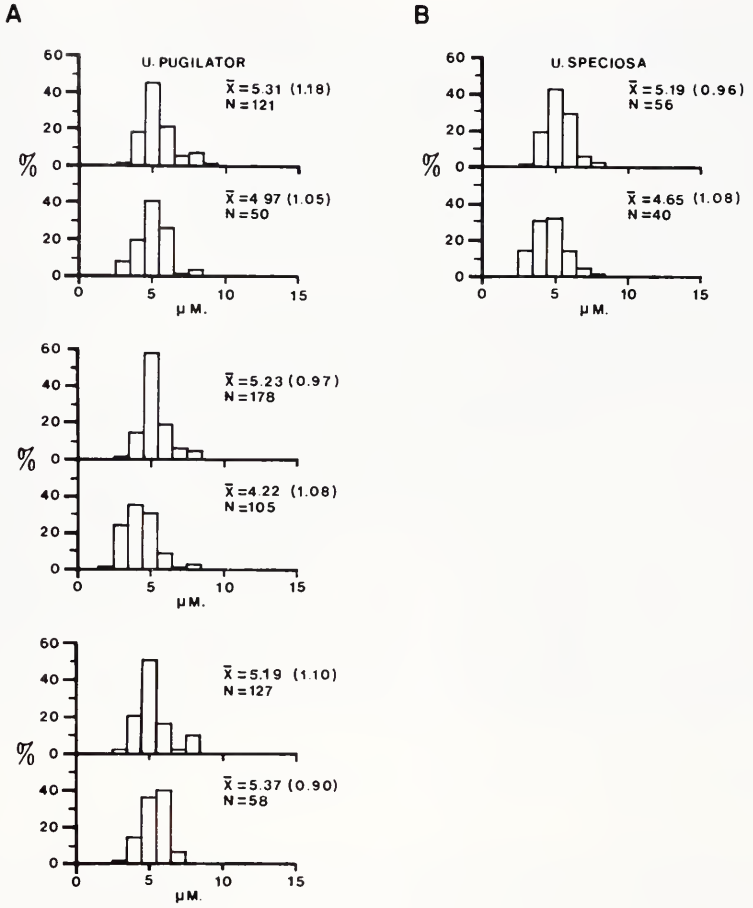


FIGURE 3. Comparisons of A-band lengths in major (upper figures) and minor (lower figures) levators of representative adult males of the subgenus *Celuca.* A: *Uca pugilator,* top to bottom, (CL = 16.6 mm, 16.9 mm, 14.8 mm). B: *U. speciosa,* (CL = 11.3 mm). $\bar{X}$ = mean A-band length (and SD) in μm from measurements of N fibers.

lengths for major/minor promotors were 7.45 μm/6.42 μm, and for major/minor depressors were 8.99 μm/6.69 μm. Both comparisons were highly significant. Data for promotor and depressor muscles have not been taken for the other five species.

No asymmetry is evident in female fiddler crabs. Figure 2 gives A-band lengths from the two minor (right and left) levator muscles of an adult female *U. minax.* Means and distributions are very similar for both muscles; differences are not significant.

Muscles of the cheliped

The cheliped consists of seven segments: coxa, adjacent to the body; basis and ischium (fused); merus; carpus; propus; and dactyl. The moveable dactyl opposes the pollex, a distal projection of the propus, forming a claw or chela. The cheliped contains six major muscles; four of these, the extensor, stretcher, flexor, and bender, effect

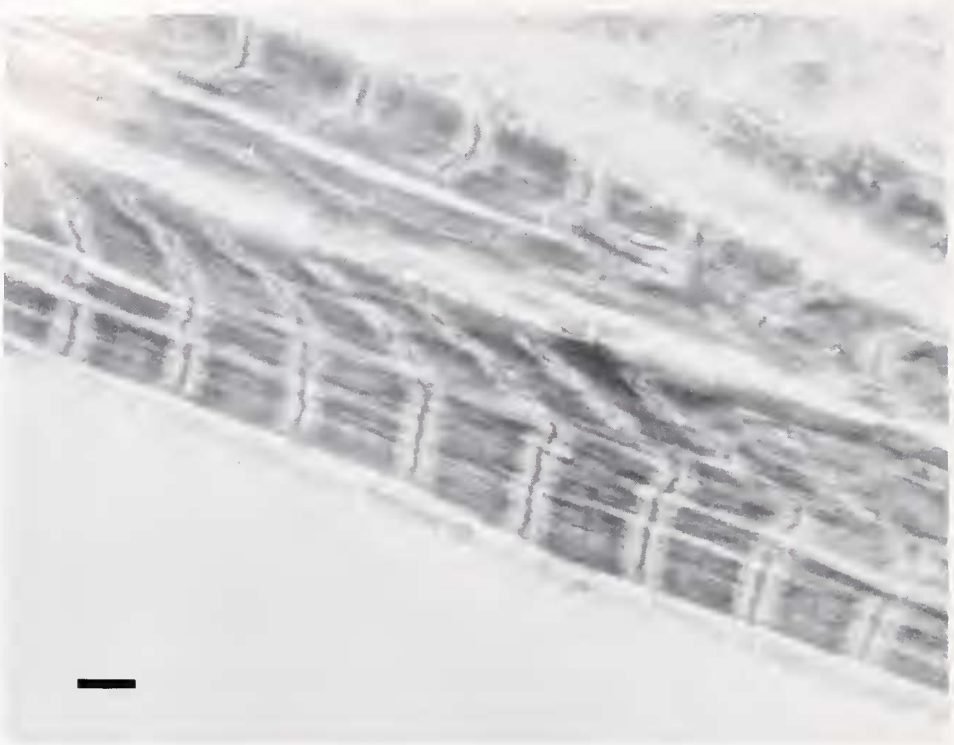


FIGURE 4. *Uca minax* major levator muscle fibers with 20–21 μm sarcomeres. FAA; 8 μm paraffin section; Mallory's triple stain; phase contrast. Scale bar = 10 μm.

extension and flexion of the limb during courtship waving. Contraction of the largest of the major chela muscles, the extensor located in the merus, causes extension of the chela at the merocarpopodite joint, a major element of the chela wave. The smaller flexor muscle, also located in the merus, is antagonistic in action to the extensor.

TABLE II

A-band measurements from fibers of remotor muscles from adult male fiddler crabs

		Major				Minor			
Species	CL	$\bar{X}$	SD	R	n	$\bar{X}$	SD	R	n
Uca minax	18.0	6.59	0.84	4–8	72	5.89	0.89	4–8	48
U. pugnax	12.0	6.92	1.31	5–11	67	5.70	1.15	5–11	43
U. rapax	13.5	7.46	1.15	5–11	92	6.24	0.92	4–9	53
U. longisignalis	15.7	6.61	0.90	4–9	78	5.32	0.93	3–7	62
U. thayeri	16.8	6.62	1.22	4–9	80	5.70	0.88	4–8	41
U. pugilator	15.9	7.40	0.85	6–9	63				
	14.3					6.45	1.00	5–8	58
U. speciosa	11.3	6.72	0.71	5–8	70	5.36	1.03	3–8	35

CL = carapace length in mm, n = number of fibers measured, major = hypertrophied cheliped, minor = other cheliped. Means ($\bar{X}$), standard deviations (SD) and ranges (R) in μm.

Contraction of the stretcher muscle in the carpus, causes extension of the chela at the carpopropodite joint, the bender muscle operates antagonistically to it. The muscles in the minor chela are similarly arranged, but there is a significant difference in its articulation. On the major side the contractions of the extensor and stretcher muscles cause the entire cheliped to be extended in a single plane, an essential component of the display wave of many species of *Uca*. On the minor side, the stretcher muscle causes a movement nearly perpendicular to that caused by the extensor muscle. Cheliped musculature in *U. pugnax* is illustrated and described in detail by Spirito (1970).

The weights and weight-ratios of cheliped muscles in two male *U. minax* and a male *U. pugilator* are given in Table III. In both species the extensors, stretchers, and benders of the major chelipeds are approximately 20 times larger than those of the minor contralateral chelipeds. Major flexor muscles of both species were approximately five times larger than their minor counterparts. In these animals the entire major chelipeds weigh 17–22 times the minor cheliped, and account for 32–47% of the entire body weight.

Figure 5 illustrates data from two male *U. minax*. The stretcher and bender muscles in the major carpus (upper half of each figure) have significantly greater mean A-band lengths than those of the minor carpus ($P < 0.05$). However, the extensor and flexor A-band lengths are indistinguishable between the major and minor chelae. For another *U. minax* (CL = 18.3 mm) data for both major and minor stretcher A-band lengths had means of 7.56 μm (SD 1.37, n = 38) and 5.41 μm (SD 0.84, n = 29) respectively; highly significant using student's *t*-test ($P < 0.001$). For a male *U. pugilator* (CL = 16.9 mm) mean A-band lengths in the major and minor flexor muscles were 6.52 μm (SD 0.82, n = 28) and 5.34 μm (SD 0.99, n = 51) respectively, again highly significant by student's *t* test ($P < 0.001$).

Variability of muscle fibers

Both A-band and sarcomere lengths were measured from the same fibers of the 15 thoracic and seven limb muscles which manipulate the chelipeds, of *U. minax*, *U. pugilator*, and *U. pugnax*. There was considerable variability in the ratio between these two length measurements, ranging from 0.46 to 0.68 (mean: 0.56) for thoracic muscle fibers and from 0.55 to 0.67 (mean: 0.59) for limb muscle fibers. These data are consistent with the suggestion that measurements of entire sarcomeres are more

TABLE III

Chela muscle weights (mg) from three Uca *(same individuals as in Table I)*

Species	CL	Major/minor chela muscle weights (major/minor ratio)			
		Extensor	Flexor	Stretcher	Bender
U. minax	20.7	228.0/16.5 (13.8)	47.1/8.0 (5.9)	112.0/5.0 (22.4)	49.6/3.6 (13.8)
U. minax	19.9	156.0/11.1 (14.1)	36.9/9.0 (4.1)	72.6/3.9 (18.6)	34.6/3.1 (11.2)
U. pugilator	13.8	58.5/6.2 (9.4)	10.0/3.7 (2.7)	34.0/1.4 (24.3)	15.1/0.8 (18.9)

CL = carapace length (mm); the "ratio" values, weight of the specified major chela muscle divided by weight of the homologous minor chela muscle, are shown in parentheses below each weight value.

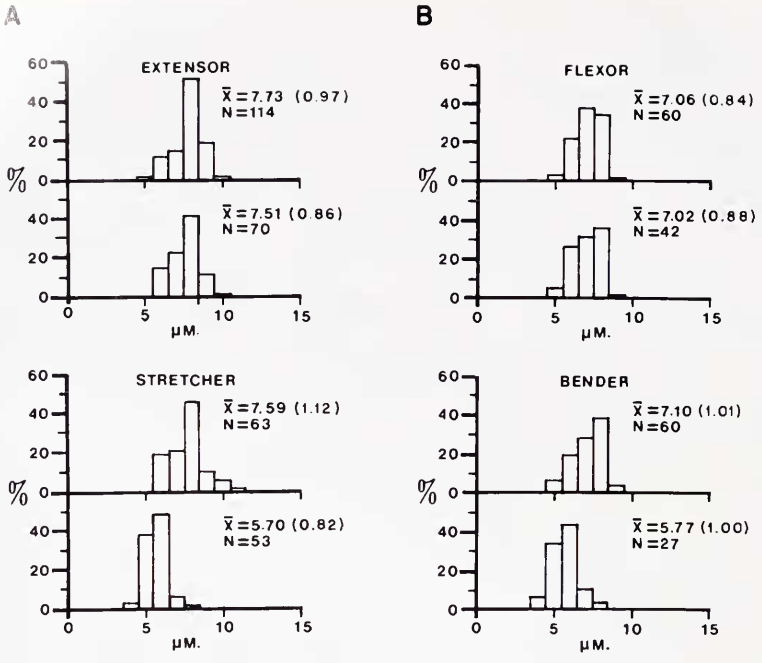


FIGURE 5. Comparisons of A-bands lengths in major (upper figures) and minor (lower figures) chela muscles from two adult male *U. minax*. A: (CL = 19.4 mm), extensor and stretcher; B: (CL = 19.9 mm), stretcher and bender. $\bar{X}$ = mean A-band (and SD) in μm, from measurements of N fibers. For major extensors and stretchers only 20% of all fibers were measured.

prone to artifactual variability due to fiber stretch during fixation (Franzini-Armstrong, 1970), the thoracic muscles being more difficult to position for fixation. For this reason only A-band measurements are used elsewhere in this report.

To estimate variation in length of A-bands from single fibers, multiple A-band measurements were made along the longitudinal axes of 12 representative fibers from levator muscles of four specimens of three species of *Uca* (Table IV). At a given point on a fiber, variation in A-band length was insignificant in the direction of the short axis, but along the longitudinal axis variation was substantial, with longer A-bands at the ends of the fibers. The Coefficient of Variation (CV) of each fiber is not related to mean A-band length for different muscle fibers from the same individual. The data presented (Table IV) show substantial variability within fibers, with CV values ranging from 7.0 to 18.8. In other data (Rhodes, 1977) there is even greater variability *between* fibers of a muscle. However CV values show no discernable trends between muscle A-bands of the major or minor sides, or between species. For example, in a comparison of the major levators of four large *U. minax* (mean CL: 20.1 mm) and four *U. pugilator* (mean CL: 16.1 mm), mean A-band lengths were 8.92 μm and 5.49 μm respectively. CV values for these means were 22.3 and 20.6.

Isometric tension

In preliminary comparisons of rates of isometric tension development in major levators of *U. minax* and *U. pugilator,* the major levator muscles of *U. minax* show slow, non-facilitating tension development to stimulus frequencies of 1 Hz. At 3 Hz

TABLE IV

Variation in A-band length (μm) for single fibers of levator muscles of four Uca *of three species*

Species	Side	Fiber #	Sample	$\bar{X}$	CV	Range
U. longisignalis	major[1]	1	13	11.11	16.2	8.7–13.3
		2	15	10.97	18.8	7.2–14.1
U. minax	major[1]	1	34	7.96	11.1	6.1–9.9
		2	27	10.71	13.6	8.0–12.5
		3	15	9.88	16.2	6.1–12.2
		4	18	9.16	15.9	6.1–11.4
	minor	1	28	8.74	12.9	7.2–10.6
		2	52	5.21	18.0	3.0–6.8
		3	31	7.82	15.0	6.1–11.4
U. pugilator	major[1]	1	33	4.87	9.0	3.8–5.7
		2	19	5.30	7.0	4.6–5.7
		3	20	5.04	7.3	4.2–5.7

[1] The posterior branch of the major levator muscle was not sampled.
CV = coefficient of variation, $\bar{X}$ = mean A-band length.

the individual responses begin to fuse. At stimulus frequencies of 10 Hz and higher the muscle responds tetanically and continues to develop tension even after the stimulus is removed. In one instance a levator of *U. minax* developed a tetanic tension equivalent to 100 g, whereas levator muscles of a similar size from *U. pugilator* rarely develop tension in excess of 10 g. These latter muscles exhibit distinct twitch-like contractions at stimulus frequencies of 10–15 Hz. These responses of whole muscles are consistent with what would be predicted from their muscle fiber composition (Atwood, 1972, 1973; Josephson, 1975).

Correlation of A-band length and wave duration

Waving in fiddler crabs is species-specific in terms of the pattern, duration, frequency, smoothness, etc. (Schöne, 1961; Crane, 1975). In order to determine whether differences in waving are due to neuromuscular properties, A-band lengths were correlated with waving behavior. Since the levators, extensors and stretchers are involved in the extension and elevation of the major claw, one might expect slow wavers to have functionally slow muscles (long A-band lengths) and fast wavers to have functionally fast muscles (short A-band lengths) (del Castillo *et al.*, 1972; Josephson, 1975). No correlation should be seen between A-band lengths of the remotor muscle and wave duration since the actions of this muscle (*i.e.*, the backward movements of the claw during the wave) are aided by gravity when the front of the animal is held up by the walking legs.

Table V lists correlations between the estimated wave durations of six species of *Uca* (Crane, 1975; Salmon, 1965, 1967; Salmon and Atsaides, 1968b; Doherty, 1982) and the grand means of all A-band measurements from four muscles from the same species (Rhodes, 1977). The wave duration values are not very satisfactory; as Doherty (1982) has shown, there is a marked negative correlation between wave duration and temperature for at least two of these species—a correlation which was not considered in earlier studies. Despite this problem, the comparisons of rank are significant ($P < 0.05$) for the levator and extensor muscles. The Spearman rank correlation tests are not significant at this level for the stretcher muscle; the remotor muscle, as predicted,

TABLE V

Comparisons of moderate intensity wave durations and means of all A-band lengths for six species of Uca

	Duration				Muscle							
					Levator		Remotor		Extensor		Stretcher	
Species	Salmon[1]	Crane[2]	Doherty[3]	Rank	μm	Rank	μm	Rank	μm	Rank	μm	Rank
U. speciosa	0.50	0.38–0.5		1	4.75	1	5.89	1	5.85	1	6.21	2
U. pugilator	1.25	0.79–1.8		2	5.49	2	7.40	5	6.23	2	6.10	1
U. minax	2.5[4]	2–3[4]	4–5	3	8.92	4	6.89	4	7.57	4	7.12	4
U. pugnax	2.1–3.7	0.87–5	9–10	4	7.47	3	6.52	2	7.63	5	7.19	5
U. rapax	3.6	2.1–12		5	9.16	6	7.50	6	7.17	3	7.11	3
U. longisignalis	5.6			6	9.03	5	6.61	3	7.76	6	7.53	6
					r_s = .886 sig.		r_s = .314 n.s.		r_s = .829 sig.		r_s = .771 n.s.	

[1] Salmon (1965, 1967); Salmon and Atsaides (1968b).

[2] Crane (1975).

[3] Doherty (1982) at 25°C.

[4] Waves in response to a female. Both authors suggest longer duration for moderate intensity waves.

n.s. = not significant; r_s = Spearman rank coefficient; sig. = significant at 5% level.

shows no correlation (Table V). These results indicate that the functional properties of the peripheral neuromuscular system correlated with sarcomere length may constrain the spatio-temporal components of the wave display and thus play a role in shaping the evolution of this species-isolating mechanism.

Discussion

The major internal modifications of the skeleton, muscles, and nervous system necessary to accommodate the great chela of male *Uca* include an asymmetry of the thoracic skeleton, a marked asymmetry in the thoracic ganglionic mass of the central nervous system (Huxley, 1932; Rhodes, 1977; Young and Govind, 1983), significant differences in the cross-sectional area of certain large (presumably motor) axons innervating the major chela muscles (Rhodes, 1977; Young and Govind, 1983), as well as the major muscle asymmetries reported here. The thoracic musculature of *Uca* with its associated skeleton (Fig. 1) reflects the gross asymmetry of the two chelae in male crabs. The major body muscles are three-fold or more greater in weight than those of the minor side, or of the homologous muscles of females of the same size. Hypertrophied muscles within the distal parts of the chela may be 20 times larger than their minor homologues.

In the more primitive species (Crane, 1975) muscle fiber lengths increase with body size but are not significantly different between major and minor sides of individual animals, even when the major muscle is hypertrophied. Sarcomere lengths, as measured by A-band lengths, are significantly larger in the thoracic muscles that manipulate the major chelipeds, compared to their minor homologues. Since the major chela is huge relative to the rest of the body, such modifications seem appropriate to the specialized role of these muscles. Waving movements by the male fiddler crab of his major cheliped must require muscles capable of developing more tension than that required to move the relatively small minor cheliped during feeding and burrowing. A portion of this power is furnished by an increase in the size of the thoracic muscles of the major side; however, the extent of such evolutionary hypertrophy may be limited by constraints imposed by the exoskeleton. Another way that the power of these muscles could be increased is by modification of the contractile machinary. Increased sarcomere length provides for greater overlap of actin and myosin filaments, the formation of more actomyosin bonds and hence of greater tension development by individual muscle fibers. Thus increasing both the size and the sarcomere lengths of the muscles that manipulate the major chela seem appropriate evolutionary responses for fiddler crabs. In several species, and particularly in the largest species studied, *U. minax*, major levator muscles are characterized by fibers with sarcomeres in excess of 20 μm. Previously reported long sarcomeres of skeletal muscle have been shown to be extremely slow and powerful (del Castillo *et al.*, 1972; Atwood, 1973; Josephson, 1975). If these functional correlates hold true for the thoracic muscles of fiddler crabs, then on a weight-specific basis these muscles are unusually powerful but very slow as well.

In contrast to the situation in most species of *Uca*, the hypertrophied major levator muscles of *U. pugilator* and *U. speciosa* show little or no difference in A-band lengths compared to their contralateral minor levator muscles. These muscles are relatively large compared to the major levator of *Minuca* species and the fibers are also relatively long. Increased muscle size without elongated sarcomeres thus represents a substantial evolutionary specialization by members of the *Celuca* sub-genus, to allow manipulation of the large cheliped without sacrificing speed, permitting faster waves and sound production. Sound production by vertical drumming of the flexed major cheliped at frequencies of 6–10 Hz (Salmon and Atsaides, 1968b; Salmon *et al.*, 1978) is characteristic of the *Celuca* subgenus, but not of the subgenus *Minuca* (see Crane, 1975).

The latter species raise and lower the flexed major cheliped at no more than 1 Hz when courting. Thus it appears that the functionally slow but powerful thoracic muscles of *U. tetragonon* and other primitive *Uca* preclude the ability to drum at a frequency that would produce sound.

These findings from species of *Uca* are supportive of the hypothesis that motor patterns generated in the central nervous system are very conservative evolutionarily, so that species-isolating behaviors are affected by more malleable peripheral elements, including the morphological and physiological properties of the muscle fibers and their associated motor axons. As Hoyle (1976) has pointed out, in supporting this possibility, "Why, otherwise, would there be such diversity in the muscles?" In the case of *Uca* the degree of muscle dimorphism could determine the duration and frequency of the courtship wave. The capacity for sound production in *Celuca* species could be determined by the type of muscle hypertrophy they have evolved to manipulate their huge major chela.

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